

Towards a reefscape ecology: relating biomass and trophic structure of fish assemblages to habitat at Davies Reef, Australia

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ABSTRACT: The complex relationship between coral reef fish assemblages and reef habitats at Davies Reef, a middle-shelf reef in the Great Barrier Reef, Australia, was approached from a reefscape perspective. A reefscape merges the spatial patterns found in a reef with 3 ecological components: structure, function and change. The main objective of this study was to explore the relationship between function (biomass and trophic structure of fish assemblages) and structure (reef habitat) within a reef. Three reef fish groups were defined using multi-dimensional scaling, and their similarity was evaluated using SIMPER analysis. From the benthic surveys conducted at the same sites we defined 3 reefscales: A, 'encrusting non-*Acropora*', B, '*Acropora*' and C, 'low density massive non-*Acropora*'. Reefscape A was characterised by maximum fish species richness and biomass, while maximum fish diversity was found in Reefscape B. Reefscape C had the minimum values of fish biomass. The relationship between fish groups (using biomass as a proxy) and habitat was explored using redundancy analysis, which was also used to identify significant fish species within each reefscape. The relationship between the trophic structure (guilds) and habitat was explored using the 4th corner analysis, and this analysis revealed that substratum types differed in terms of their utility as proxies for associated fish species and trophic guilds. The present study stresses the importance of within-reef variability as a determinant of composition and relative abundance of local reef fish assemblages. It also suggests that, while loss or change of habitat structure (i.e. coral cover or change in the dominant coral type) could reduce species richness and biomass, some of the habitat features to which fishes cue are probably coarser geomorphological and environmental zones.

KEY WORDS: Reef habitat · Biomass · Trophic structure · Coral reef fishes · Great Barrier Reef · Biodiversity · Complexity

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INTRODUCTION

The term 'landscape' is used to describe any spatially heterogeneous terrestrial area in terms of characteristics of structure, function and change (Turner & Gardner 1991). Here, 'structure' refers to the spatial

relationships between distinctive habitats within the prescribed area, and 'function' refers to the interaction between spatial elements, notably the flow of energy, materials and organisms among the component habitats. 'Change' refers to alteration in the structure and function through time. The variability across

and around large coral reefs may also be considered in similar terms. We use the term 'reefscape' to describe spatially discrete elements of morphological and biological structure of a coral reef to enable exploration of the complex relationships between the fixed physical structure (including benthic organisms such as corals) and its most conspicuous motile component, the reef fishes.

How well reef benthic composition, diversity, abundance and/or structural complexity might predict reef fish composition and diversity has been the focus of numerous studies (Risk 1972, Gladfelter & Gladfelter 1978, Gladfelter et al. 1980, Carpenter et al. 1981, Roberts & Ormond 1987). Heterogeneity and complexity in reef fish habitat, manifesting as local differences in food, shelter and mating sites (Caley et al. 2001), are important determinants of pattern and diversity in reef fish assemblages (Grigg 1994, McCormick 1994, Ault & Johnson 1998, Nuñez-Lara & Arias-González 1998, Jones & McCormick 2002, Nuñez-Lara et al. 2005). Such local habitat characteristics can also set an upper limit on local fish population sizes, affect the magnitude of fish recruitment in space and time, and modify patterns of juvenile fish growth (reviewed in Jones & McCormick 2002). Not surprisingly, not all habitat characteristics are equally important in influencing reef fish communities (Legendre et al. 1997, Jones & Syms 1998).

'Coral reef habitat' is rarely defined explicitly, and often mixes geomorphology (e.g. crest, back reef, or spur and groove zone) and biotic cover (e.g. *Porites* spp., turf algae) and substrate irregularity (e.g. heterogeneity, complexity, rugosity). There is also little uniformity in the scales or use of habitat classification (Jones & Syms 1998), which has led to confusion in interpretation (Mumby & Harborne 1999) and does not allow easy direct comparisons of studies. Nor can it be assumed that fishes are responding to the same spatial units as perceived by human observers.

Increasingly, studies are separating benthic and geomorphic attributes in the development of coral reef habitat classifications (Chancerelle 1996, Phillips et al. 1997, González-Gándara et al. 1999, Mumby & Harborne 1999). Habitats are defined exclusively according to ecological attributes (biotic cover), and the associated geomorphologic classes are then assigned to each habitat class. This is the approach adopted in the present study. We classified reef fish assemblages from a wide range of habitats within Davies Reef on the Great Barrier Reef (GBR) and looked for habitat characteristics that were associated with the attributes of each reef fish assemblage. In doing so we investigated the 2 reefscape characteristics: structure (habitat) and function (the biomass and trophic structure of fish assemblages that is sustained by that structure).

MATERIALS AND METHODS

Study area. Davies Reef (18°50'S, 47°39'E; Fig. 1) is a mid-shelf reef located in the central section of the GBR (Done 1982, Riddle et al. 1990). Mid-shelf reefs in this section of the GBR are located 50 to 80 km from the coast. Davies Reef has a typical geomorphologic profile for reefs on the GBR: slope, crest, reef flat and lagoon with patch reefs (or 'bommies'), and has a steeply sloping reef front dropping to depths of ca. 50 m (Bradbury et al. 1986). Behind the reef front is an extensive lagoon (6 to 15 m depth), which comprises approximately 50% of the reef's area, largely open to the west and bounded to the southeast by a 300 m wide intertidal reef flat. The outer reef slope is gradual in the windward sector (SW/S/SE sectors) and steep in the more sheltered sector (SW/N/SE). Inside the lagoon there is a complex maze of reef structures, including a conspicuous shelf of sand with intertidal reef patches. The prevailing winds and associated waves in this region are from the southeast (Riddle et al. 1990).

Sampling. We surveyed benthos and fishes from 7 to 12 May 2002, using 54 fish and video sampling stations (Fig. 1). Sites were selected from an aerial photograph (1:5000) to maximise the range of habitats surveyed (reef slopes, shelves and submerged patch reefs). Fish and benthos were censused using transects laid at depths we believed would best characterise habitat features used by fishes, viz. towards the mid-range depth of the sides of bommies (1 to 10 m depth), the reef slope (1 to 8 m depth), or submerged shelf areas (1 to 6 m depth) and also in the shallower parts of these areas (typically <1 m). At each station, fish were visually censused either by snorkelling (for sites less than ~2 m) or by SCUBA (greater than ~2 m). First, a transect line was positioned along the chosen depth contour, and then 2 passes were made, the first recording large mobile reef fishes, and the second, small and juvenile fishes. All fishes were categorised by species and length classes. Large fish (>10 cm length) were categorised into 10 cm categories, while small and juvenile fishes (≤10 cm length) were categorized as <2 or 2–10 cm.

We converted fish lengths to biomass (g wet weight m^{-2}) using the allometric equation $W = aL^b$. The constants for each species were obtained from FishBase (www.fishbase.org/home.htm) or, if the species in question was not logged in FishBase, from a species with a similar shape. For each species, total biomass per census was estimated as the average weight multiplied by the abundance.

The benthic community at each site was surveyed using an underwater video camera to record a 40 cm wide swathe along each 50 m transect. The camera was held approximately 50 cm to the side of the tape

and approximately normal to the substrate. Each video transect was then sampled using 200 systematically dispersed points (Page et al. 2001). The benthos under each point sampled was identified to the lowest taxonomic group and life form possible. For some analyses, data were grouped into the following major benthic categories: hard coral, soft coral, coralline algae, macro-algae, turf algae, sponge and other benthos. A combination of morphology and taxonomic grouping was considered the most appropriate for the purposes of this study, with the assumption that reef fish communities, overall, are more likely to be associated with coral growth forms than with particular coral species.

Classification of fish assemblages and habitats.

Fish transect information was compiled into a matrix (species biomass by transect) and used to compute Bray-Curtis similarity among all transects. We used non-metric, multi-dimensional scaling analysis (MDS; Clark 1993) on transformed square root fish species biomass to generate groups of fish assemblages. We then conducted a non-metric, 1-way, pairwise analysis of similarity (ANOSIM; Clark & Warwick 1994) among the groups, and a SIMPER analysis (Clark & Warwick 1994) to determine which species contributed most to the similarities and differences among the fish assemblages. We then characterised each fish assemblage using: biomass and trophic structure. For biomass, we used redundancy analysis (RDA) and Monte Carlo permutation tests (Program CANOCO, Ter Braak & Smilaur 1998) on Hellinger transformation of the fish species biomass data. Legendre & Gallagher (2001) have shown that this transformation makes species abundance data amenable to analyses like principal component analysis (PCA) or RDA. We performed an RDA analysis for 3 fish assemblages against habitat characteristics, and to examine fish trophic structure we used 4th corner analysis (Legendre et al. 1997). This latter technique detects associations between trophic structure and habitat, as well as testing their significance using permutations. In our case, the 2 underlying assumptions for the tests are: (1) that all fish species are found at locations where they encounter appropriate living conditions; and (2) that they do so independently of each other (Model I in Legendre et al. 1997). We allo-

cated each fish species to 1 of 6 trophic categories: 1 = fish feeders (F), 2 = macro-invertebrate feeders (Ma), 3 = micro-invertebrate feeders (Mi), 4 = zooplankton feeders (Z), 5 = macro-algal feeders (H1), 6 = micro-algal feeders (H2) and 7 = coral feeders (C). Species were assigned to these categories based on data obtained from Kulbicki et al. (1994).

RESULTS

A total of 206 species of reef fishes (202 identified and 4 unidentified) were recorded in the 54 transects surveyed at Davies Reef. The most common families

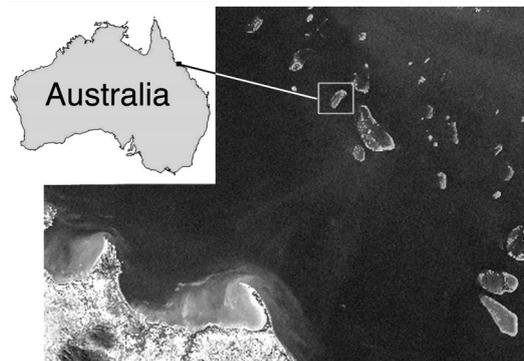
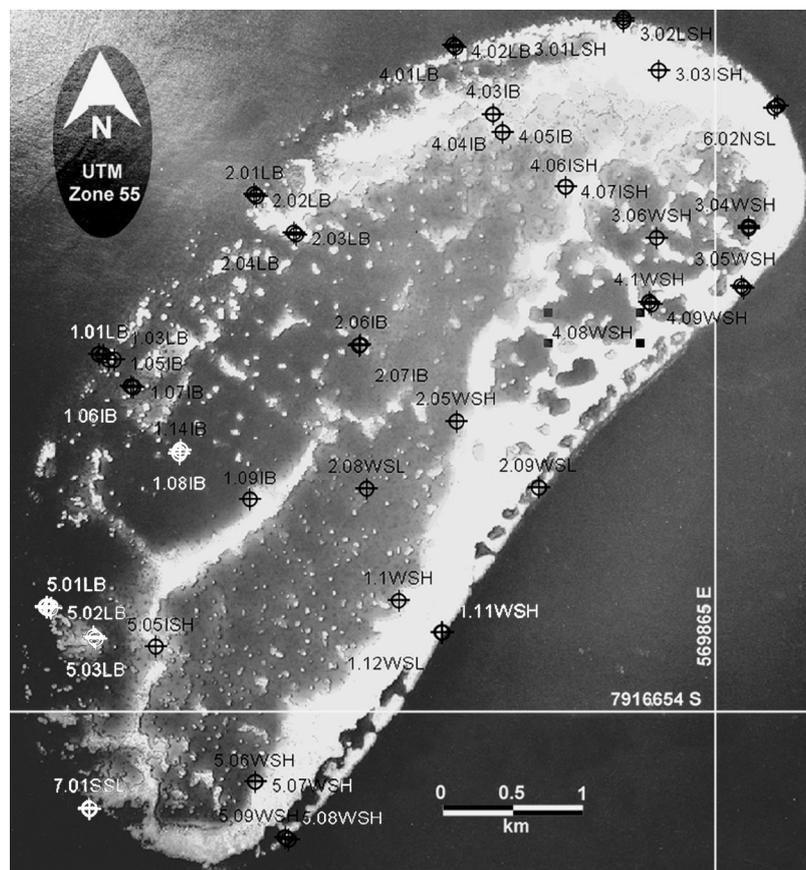


Fig. 1. Study area, Davies Reef, Great Barrier Reef, Australia. Numbers represent line transects surveyed through the reef and letters represent position on the reef (L: leeward; W: windward; I: inner) and geomorphologically associated structures (SL: slopes; B: bommies; SH: shelf)

were the Pomacentridae, Labridae, Chaetodontidae, Acanthuridae, Scaridae and Serranidae. Fish biomass m^{-2} averaged ($\pm SE$) $246 \pm 18 g$ wet weight m^{-2} , and fish abundance averaged ($\pm SE$) 37 ± 0.99 fishes m^{-2} . Species incidence was extremely patchy across transects, with the majority of species represented in only a few transects, in fact more than half of all species occurred in <5 transects. No species were represented in all 54 transects, and only 20 species occurred in more than half of all transects. Forty-eight species (24%) were present in only 1 transect; 22 species, in 2 (11%); and 12, in 3 (6%). Most species were also rare and had extremely low biomasses m^{-2} ($<1 g m^{-2}$). The average biomass of even the most dominant species (the small damselfish *Neopomacentrus azysron*) was still low, at only $24 g m^{-2}$. The 5 most important species, in terms of their frequency and biomass, belonged to the family

Pomacentridae (*Pomacentrus lepidogenys*, *Neopomacentrus azysron*, *Pomacentrus moluccensis*, *Acanthochromis polyacanthus* and *Pomacentrus bankanensis*).

The MDA analysis (Fig. 2) suggested that the fish species at Davies Reef can be split into 3 main assemblages or groups. These groups, while overlapping in their species composition (Table 1), do segregate to some extent according to depth (Fig. 2a) and total coral cover (Fig. 2b; intergroup differences significant at $p < 0.05$ in ANOSIM analysis), but also the cover of specific coral groupings. For convenience, we labelled each reefscape after prominent benthic features: A, 'encrusting non-*Acropora*', B, '*Acropora*' and C, 'low density massive non-*Acropora*'.

An independent hierarchical cluster analysis using the fish data only (Fig. 3) produced essentially the same site groupings as the MDA analysis. In both methods, shelves (Sh), bommies (B) and slopes (Sl) had a tendency to cluster together, with patterns that also appeared to relate to reef aspect. For example, Cluster A contained mainly transects from the slope and bommie sites (6 m average depth, 10 m maximum depth). Cluster B contained mainly shelf transects, with only a few bommie and slope sites (2 m average depth). Cluster C included bommie, shelf and slope sites (4 m average depth).

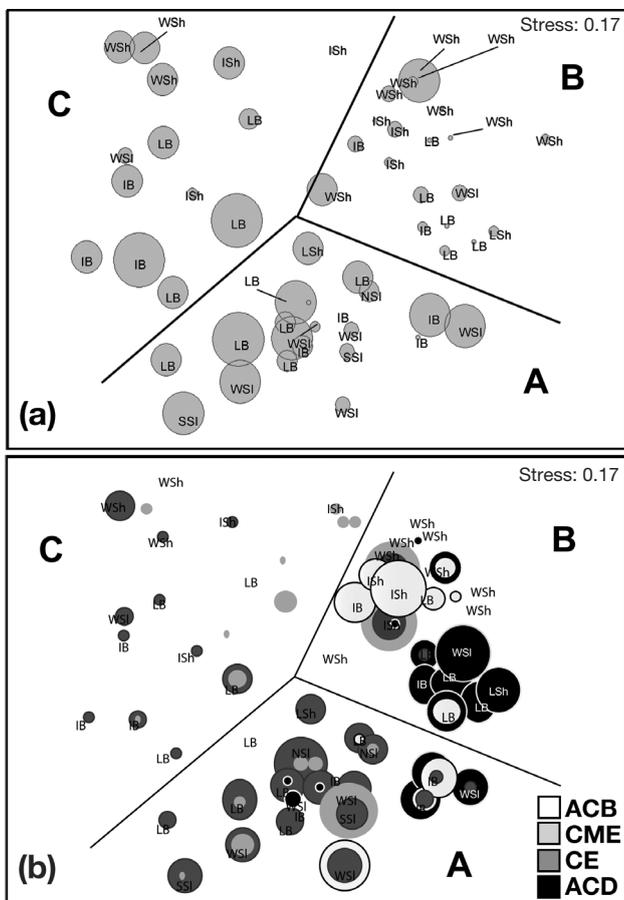


Fig. 2. Multi-dimensional scaling (MDS) ordination of the 54 transects, based on fish species biomass (measured by Bray-Curtis similarity coefficient). Reefscapes A, B and C labelled. (a) Symbol sizes represent maximum depth of each transect (larger symbols being deeper). (b) Symbol sizes represent percentage morphotypes cover in each transect (CE: coral, encrusting [non-*Acropora*]; CME: coral, *Millepora* encrusting; ACB: branching *Acropora*; ACD: digitate *Acropora*)

Cluster A: The encrusting non-*Acropora* reefscape and associated fishes

This reefscape is dominated by encrusting non-*Acropora* corals (typically $>20\%$ cover; Fig. 4), with *Acropora* and soft corals typically occupying <7 and 3% of the benthos, respectively, and with low coverage of zoanthids and sponges (typically <2 and 1% , respectively). The reefscape is relatively free of sand, and with relatively low coverage of turf algae (mean coverage $<37\%$) and moderate coverage of calcareous and other algae (14 and 12% , respectively) compared to the other reefscapes.

Fish biomass averaged ($\pm SE$) $322 \pm 37 g$ wet weight m^{-2} (Fig. 4), while a total of 134 and an average of 40 species per transect were recorded. Pomacentrids were the dominant family, in terms of mean ($\pm SE$) biomass and species richness ($161 \pm 22 g$ wet weight m^{-2} and 13 ± 0.90 species, respectively; Fig. 5a, b). Species from the genera Labridae, Scaridae, Chaetodontidae and Acanthuridae were also conspicuous. *Pomacentrus lepidogenys* and *Neopomacentrus azysron* are diagnostic fish species of this reefscape (35.56 and 12.21% contributions to within-group similarities in SIMPER analyses), while *Pterocaesio marri* (3.90% of within-group similarities), *Pomacentrus brachialis* (3.33% of within-group similarities) and *Ctenochaetus*

striatus (3.27% of within-group similarities) are also notable species (Table 1, Cluster A). A total of 32 species contributed to 90% of within-group similarities within this reefscape.

Within each reefscape, subsets of substratum types were associated with distinctive subsets of fish species. For the fish assemblage overall, Monte Carlo permutation test revealed 2 significantly correlated benthic variables (Table 2): the highest biomass values of both *Pomacentrus lepidogenys* and *Neopomacentrus azysron* were associated with encrusting non-*Acropora* (CE) and *Millepora* (CME), whereas the highest biomass value of *Pterocaesio marri* was associated with branching non-*Acropora* (CB) and zoanthid (ZO) (Fig. 6a). Fish families in Reefscape A did not partition themselves across 3 growth forms of *Acropora* (table,

encrusting and branching), although different species within those families did. For example, *Pomacentrus bankanensis*, *Thalassoma hardwicke*, *Thalassoma amblycephalum* and *Scarus globiceps* were consistently partitioned across coralline algae (CA), *Halimeda* (HA), sub-massive non-*Acropora* (CS) and tabulate *Acropora* (ACT), while *Neopomacentrus azysron*, *Pomacentrus lepidogenys*, *Abudefduf whitleyi* and *Scarus niger* were consistently partitioned across encrusting non-*Acropora* (CE) and *Millepora* (CME).

In terms of trophic groups, zooplankton feeders were by far the most dominant trophic category in Reefscape A (mean \pm SE biomass per transect: 240.75 \pm 34.69 g wet weight m⁻²; Figs. 4 & 7). Plant and micro-invertebrate feeders also made significant contributions to biomass (mean \pm SE: 40.6 \pm 5.05 and 15.2 \pm 1.75 g wet weight m⁻²,

Table 1. Species causing intra-group similarities (70% cum.) and inter-group dissimilarities (50% cum.) based on Bray-Curtis similarity and dissimilarity in Reefscape A, B and C. Species are ordered in decreasing percent contribution (Contrib.)

Species	Contrib. %	Cum. %	Species	Contrib. %	Cum. %
Cluster A Average similarity = 31.35			Clusters A & B Average dissimilarity = 85.15		
<i>Pomacentrus lepidogenys</i>	35.56	35.56	<i>Pomacentrus lepidogenys</i>	12.87	12.87
<i>Neopomacentrus azysron</i>	12.21	47.77	<i>Neopomacentrus azysron</i>	10.72	23.59
<i>Pterocaesio marri</i>	3.90	51.67	<i>Pomacentrus bankanensis</i>	4.54	28.13
<i>Pomacentrus brachialis</i>	3.33	55.00	<i>Pterocaesio marri</i>	4.48	32.61
<i>Ctenochaetus striatus</i>	3.27	58.27	<i>Cirrhilabrus punctatus</i>	3.93	36.54
<i>Thalassoma lunare</i>	3.09	61.35	<i>Pomacentrus chrysurus</i>	3.91	40.45
<i>Scarus niger</i>	2.95	64.30	<i>Chromis agilis</i>	3.81	44.26
<i>Pomacentrus moluccensis</i>	2.91	67.22	<i>Acanthochromis polyacanthus</i>	3.71	47.97
<i>Pomacentrus philippinus</i>	2.62	69.84	<i>Pomacentrus moluccensis</i>	3.27	51.24
Cluster B Average similarity = 33.05			Clusters B & C Average dissimilarity = 87.20		
<i>Pomacentrus chrysurus</i>	12.70	12.70	<i>Pomacentrus moluccensis</i>	6.36	6.36
<i>Pomacentrus bankanensis</i>	9.77	22.47	<i>Chrysiptera rollandi</i>	5.78	12.13
<i>Pomacentrus wardi</i>	6.95	29.42	<i>Pomacentrus bankanensis</i>	5.24	17.38
<i>Acanthochromis polyacanthus</i>	6.16	35.58	<i>Pomacentrus chrysurus</i>	4.86	22.24
<i>Pomacentrus moluccensis</i>	6.06	41.64	<i>Acanthochromis polyacanthus</i>	4.46	26.69
<i>Chlorurus sordidus</i>	5.95	47.60	<i>Chromis agilis</i>	4.26	30.95
<i>Thalassoma lunare</i>	4.57	52.17	<i>Cheilodipterus quinquelineatus</i>	4.06	35.00
<i>Thalassoma hardwicke</i>	4.38	56.54	<i>Pomacentrus brachialis</i>	3.27	38.27
<i>Chromis agilis</i>	4.26	60.80	<i>Assessor macneili</i>	2.72	43.97
<i>Halichoeres melanurus</i>	3.60	64.40	<i>Neopomacentrus azysron</i>	2.26	46.23
<i>Scarus rivulatus</i>	3.56	67.96	<i>Pomacentrus wardi</i>	2.14	48.37
<i>Dischistodus pseudochrysoeocilus</i>	3.05	71.02	<i>Cirrhilabrus punctatus</i>	2.12	50.49
Cluster C Average similarity = 28.49			Clusters A & C Average dissimilarity = 84.57		
<i>Chrysiptera rollandi</i>	25.01	25.01	<i>Pomacentrus lepidogenys</i>	13.54	13.54
<i>Pomacentrus moluccensis</i>	20.06	45.07	<i>Neopomacentrus azysron</i>	11.15	24.69
<i>Assessor macneili</i>	6.68	51.75	<i>Pomacentrus moluccensis</i>	5.09	29.79
<i>Pomacentrus brachialis</i>	4.91	56.66	<i>Cirrhilabrus punctatus</i>	5.04	34.82
<i>Cheilodipterus quinquelineatus</i>	3.44	60.11	<i>Pterocaesio marri</i>	4.85	39.67
<i>Choerodon fasciatus</i>	3.03	63.14	<i>Chrysiptera rollandi</i>	4.55	44.23
<i>Amblygobius decussatus</i>	2.46	65.60	<i>Cheilodipterus quinquelineatus</i>	3.68	47.91
<i>Caesio cuning</i>	2.45	68.05	<i>Pomacentrus brachialis</i>	3.48	51.39
<i>Pomacentrus amboinensis</i>	2.30	70.35	<i>Caesio cuning</i>	2.66	54.05

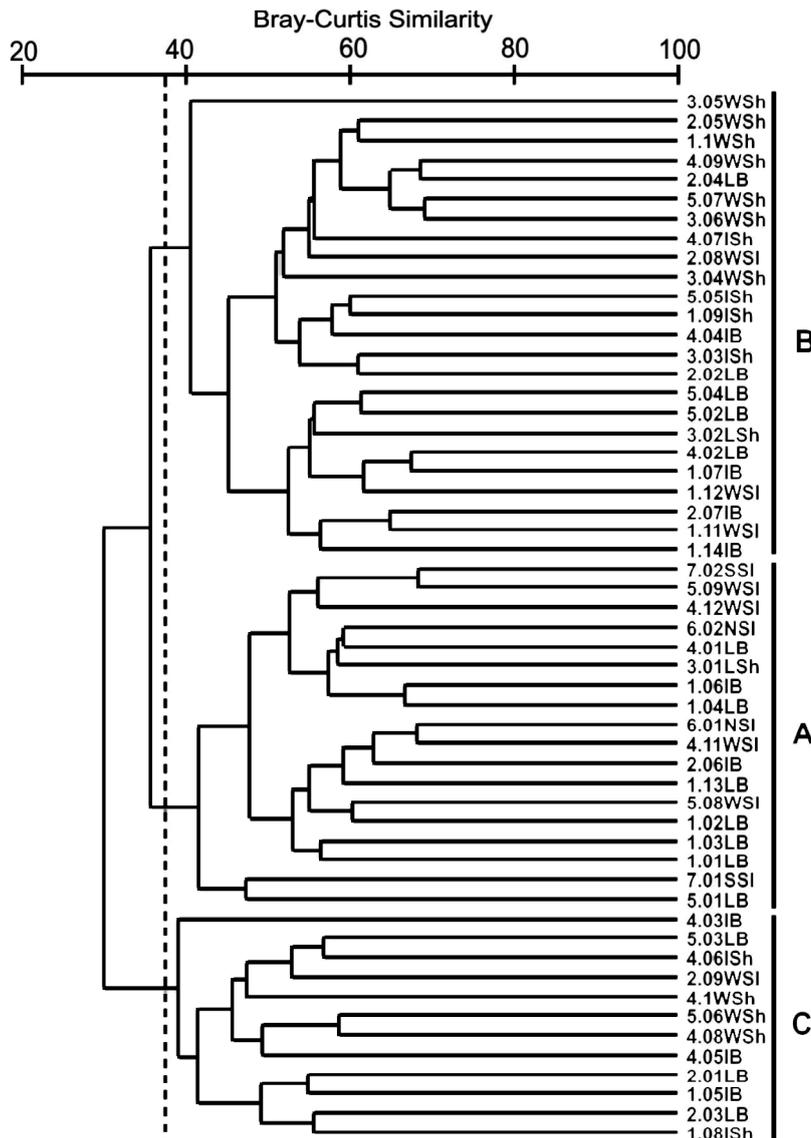


Fig. 3. Cluster analysis of the 54 transects, based on fish species biomass using Bray-Curtis similarity. Reefscapes A, B, and C labelled. Letters in cluster names represent geomorphologically associated structures (SI: slopes; B: bommies; Sh: shelf) and position on the reef (L: leeward; W: windward; I: inner)

respectively). There were 5 significant relationships between fish feeding categories and individual benthic attributes (Table 3). These were: macro-algal feeders negatively correlated to 'algae, other', 'zoanths' and 'macro-algae'; macro-algal feeders positively correlated to encrusting *Acropora*; and micro-algal feeders negatively correlated to encrusting non-*Acropora*.

Cluster B: *Acropora* reefscape and associated fishes

In Reefscape B, the cover of *Acropora* corals was the highest of the 3 reefscapes (9%; Fig. 4). The *Acropora*

added 3D complexities to a substratum with patchy sand (12%) and relatively high cover of turf algae (62%). The cover of soft corals, sponges and other invertebrates was very low (<0.40, 0.09 and 0.20%, respectively). Fish biomass averaged (\pm SE) 201 \pm 17 g wet weight m^{-2} (Fig. 4), while 118 fish species were recorded with a mean of 36 species per transect. As in Reefscape A, Pomacentrids were again the dominant family in terms of biomass (161 \pm 22 g wet weight m^{-2} ; Fig. 5a), whereas the Labridae contributed the highest number of species per transect (12; Fig. 5b). *Pomacentrus chrysurus* and *P. bankanensis* are distinguishing species in the sense that they made the highest contributions to within-group similarities (12.70 and 9.77%, respectively). Also contributing significantly were *P. wardi* (6.95%), *Acanthochromis polyacanthus* (6.16%) and *P. moluccensis* (6.06%) (Table 1). A total of 25 species made up 90% of within-group similarities. For the fish assemblage overall, Monte Carlo permutation test revealed 3 significantly correlated benthic variables (Table 2): the highest biomass of *P. chrysurus* was associated with digitate *Acropora* (ACD); the highest biomass of *P. bankanensis* was associated with sub-massive *Acropora* (ACS); and the highest biomass of *P. wardi* was associated with branching non-*Acropora* (CB), macroalgae (MA) and sponges (SP) (Fig. 6b).

Within-reefscape fish variability was associated with within-reefscape benthic variability (Fig. 6b). For example, the middle right of Reefscape B (Fig. 6b) was characterised by a variety of *Acropora* growth forms (Table 3), and a distinctive suite of Pomacentrids, Labrids and Scarids, the latter with individual species strongly associated with either coralline or turf algae. Other associations are observable in Fig. 6b.

In terms of trophic function, plant feeders, zooplankton feeders and micro-invertebrate feeders made the highest contribution to the mean (\pm SE) biomass of Reefscape B (84.81 \pm 9.34, 59.1 \pm 12.42 and 29.8 \pm 2.32 g wet weight m^{-2} per transect, respectively) (Figs. 4 & 7). Reefscape B had the highest plant-feeder biomass of all 3 seascares. Table 3 presents the correlations of feeding habits and reef benthic categories. Holm's procedure detected 7 significant relationships, in none of which the cause and

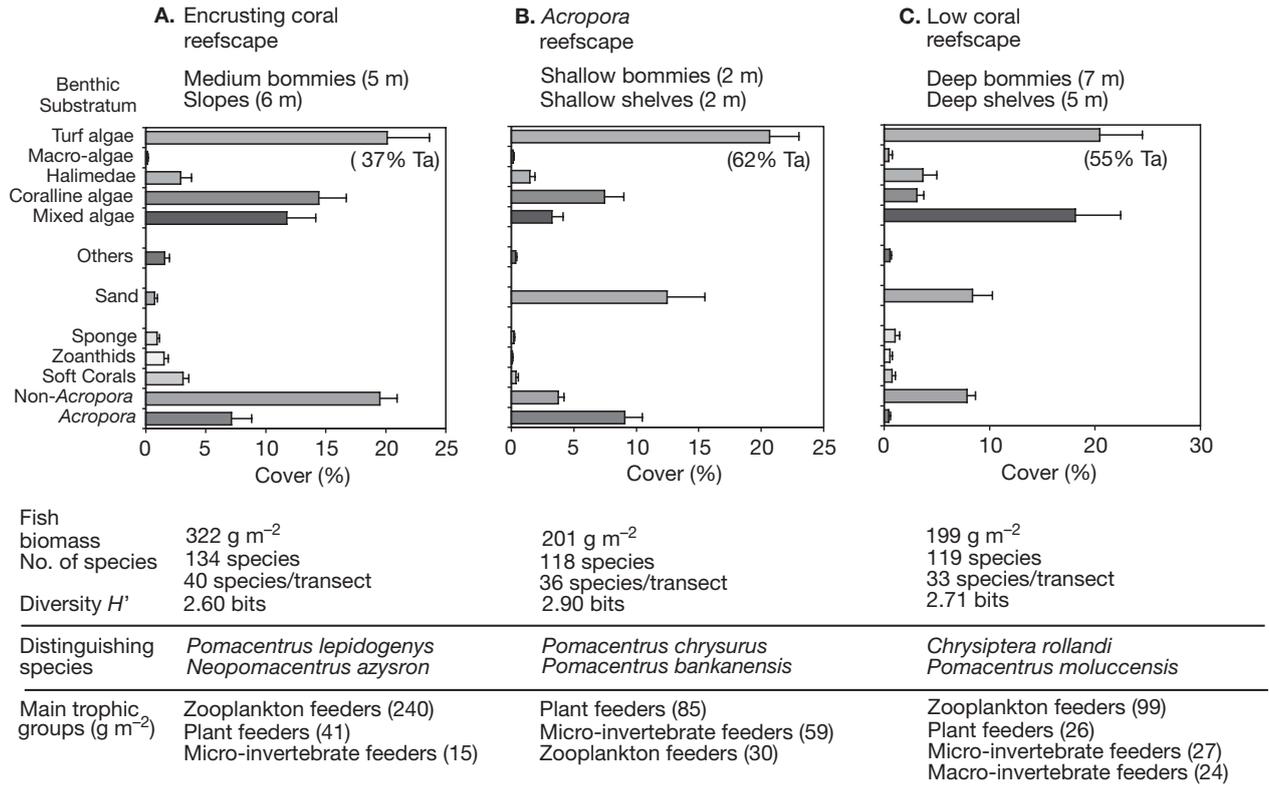


Fig. 4. Principal benthic substratum, fish characteristics (biomass, number of species, trophic groups) and dominant species associated with Reefscape A, B and C (Ta: turf algae)

Table 2. Monte Carlo permutation test of the effect of environmental variables on fish species in Reefscape A, B and C: branching *Acropora* (ACB), digitate *Acropora* (ACD), encrusting *Acropora* (ACE), sub-massive *Acropora* (ACS), tabulate *Acropora* (ACT), bottlebrush *Acropora* (ACX), other algae (AO), coralline algae (CA), branching non-*Acropora* (CB), encrusting non-*Acropora* (CE), foliose non-*Acropora* (CF), *Millepora* (CME), massive non-*Acropora* (CM), sub-massive non-*Acropora* (CS), *Halimeda* (HA), macro-algae (MA), other (OT), sand (S), soft corals (SC), sponge (SP), turf algae (TA), zoanths (ZO), unknown (UNK)

Reefscape A			Reefscape B			Reefscape C		
Variable	λ	p	Variable	λ	p	Variable	λ	p
CE	0.09	0.014	ACD	0.14	0.006	SP	0.13	0.109
CME	0.13	0.023	AO	0.09	0.016	HA	0.09	0.292
AO	0.08	0.059	ACB	0.10	0.027	TA	0.09	0.349
CF	0.07	0.083	MA	0.07	0.057	CE	0.09	0.380
ACT	0.06	0.171	CM	0.06	0.098	SC	0.08	0.391
SC	0.06	0.176	CE	0.05	0.101	S	0.08	0.427
ACD	0.05	0.197	HA	0.06	0.112	AO	0.06	0.481
CA	0.05	0.216	OT	0.04	0.215	CA	0.06	0.560
SP	0.05	0.245	SP	0.04	0.268	CM	0.06	0.582
ACB	0.04	0.246	ACE	0.04	0.342	CB	0.06	0.635
CB	0.06	0.287	S	0.04	0.407	ZO	0.05	0.786
HA	0.04	0.362	ACX	0.03	0.458			
TA	0.03	0.388	CS	0.04	0.523			
CS	0.04	0.434	TA	0.03	0.527			
CM	0.04	0.456	ACT	0.02	0.555			
OT	0.03	0.524	SC	0.03	0.594			
ZO	0.03	0.604	ACS	0.02	0.605			
S	0.02	0.684	CB	0.03	0.612			
			CA	0.02	0.647			
			UNK	0.03	1			

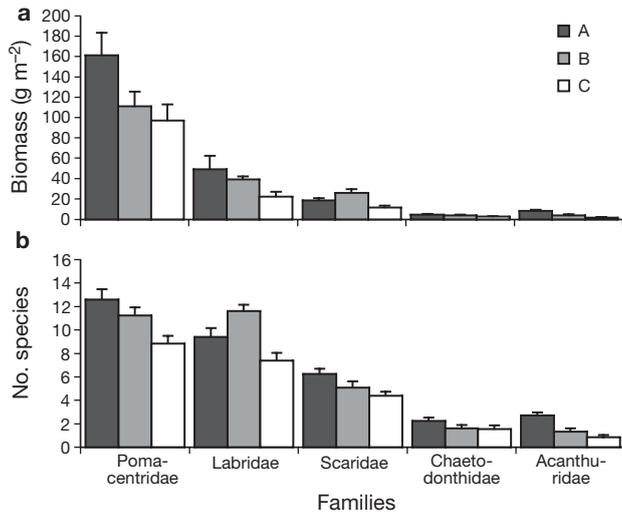


Fig. 5. (a) Biomass (g wet weight m⁻²) and (b) number of species of the 5 most important families in Reefscapes A, B and C

effect relationships are immediately obvious: zooplankton feeders negatively related to branching *Acropora*, branching non-*Acropora* and soft corals; zooplankton feeders positively related to sponges; micro-algal feeders positively related to massive non-*Acropora* and branching *Acropora*; and coral feeders positively related to massive non-*Acropora*.

Cluster C: Low coral reefscape and associated fishes

A low cover of coral (typically <8%) and medium sand cover characterised Reefscape C (Fig. 4). Of the coral present, most were non-*Acropora*, and soft corals, zoanthids and other invertebrates had negligible cover. Mixed algae and turf were both present in relatively high cover. Fish biomass was similar to that in Reefscape B but less than that in Reefscape A (199 ± 28 g wet weight m⁻²; Fig. 4). A total of 119 individual fish and an average of 33 species were recorded per transect (Fig. 4). Again, Pomacentrids were the dominant family in terms of mean (\pm SE) biomass (97 ± 15 g wet weight m⁻²) and species richness (Fig. 5). The highest contribution to the within-group similarities were made by *Chrysiptera rollandi* and *Pomacentrus moluccensis* (25.48 and 16.46%, respectively), followed by *Assessor macneili* (6.68%), *P. brachialis* (4.91%) and *Cheilodipterus parazonatus* (3.44%) (Table 1). A total of 26 species made up 90% of within-group similarities in this reefscape.

Reefscape C is characterised by various substratum types, with only loosely associated fish assemblages (Fig. 6c). No association between fish and substratum was found to be statistically significant using the Monte Carlo permutation test (Table 2). Of the 3

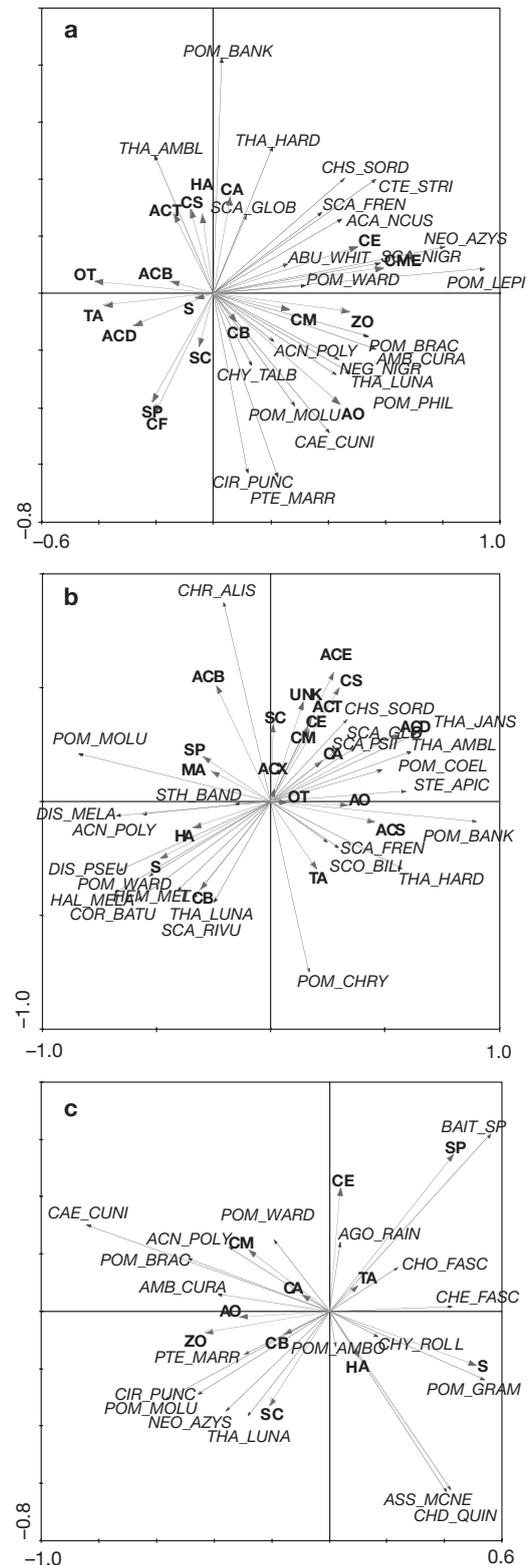


Fig. 6. Ordination diagrams of redundancy analysis in Clusters (a) A, (b) B and (c) C. Biplots of environmental variables (in bold face) and all fish species (names are formed by the 3 first letters of the genus and the 4 first letters of the species)

dominant fish species (Fig. 6c), the strongest associations between fish biomass and benthos were for *Chrysiptera rolland* with encrusting non-*Acropora* (CE); *Pomacentrus moluccensis* with *Halimeda* (HA) and *Assessor macneili* with *Halimeda* (HA) and sand (S).

In terms of trophic function, zooplankton feeders make the highest contribution of biomass in Reefscape C (99.15 ± 19.01 g wet weight m^{-2} ; Figs. 4 & 7). This is less than half the zooplanktivore biomass of Reefscape A but >3 times that of Reefscape B. Plant feeders, micro- and macro-invertebrate feeders and fish feeders make very similar contributions to the mean

(\pm SE) biomass per transect (26.23 ± 4.54 , 26.61 ± 4.56 , 23.84 ± 11.42 and 18.92 ± 10.98 g wet weight m^{-2} , respectively). There were 8 statistically significant relationships between benthic attributes and trophic classes (Table 3): zooplankton feeders negatively related to massive non-*Acropora*, sponges, *Millepora* and encrusting soft corals; zooplankton feeders positively related to digitate *Acropora*; micro-algal feeders negatively related to encrusting and caespitose soft corals; and coral feeders positively related to foliose non-*Acropora*. The ecological significance of these relationships is unclear.

Table 3. Significant relationships among feeding habits and environmental variables in Reefscape A, B and C (F: fish feeders; Ma: macro-invertebrate feeders; Mi: micro-invertebrate feeders; Z: zooplankton feeders; Hi: micro-algal feeders; Ha: macro-algal feeders; C: coral feeders). The table reports probabilities adjusted using Holm's procedure within each habitat variable (9999 permutations) (bold face: significant)

		F	Ma	Mi	Z	Hi	Ha	C
Reefscape A								
Algae other	$r(i,j)$	0.04979	0.00686	-0.01501	0.01488	-0.03439	-0.01943	-0.00502
	Prob	0.53040	0.39510	0.29160	0.28050	0.02520	0.21360	0.43170
Encrusting non- <i>Acropora</i>	$r(i,j)$	0.03449	-0.00126	0.02442	0.02573	-0.04012	-0.07781	0.05817
	Prob	0.10890	0.48490	0.17400	0.15230	0.34720	0.01520	0.42240
Zoanthids	$r(i,j)$	0.00779	0.02918	-0.01009	0.00193	-0.03618	-0.01137	-0.00618
	Prob	0.40120	0.14310	0.36020	0.47300	0.00390	0.32340	0.41640
Encrusting <i>Acropora</i>	$r(i,j)$	-0.04150	-0.00268	-0.00959	-0.01266	0.15340	0.02355	-0.02063
	Prob	0.04390	0.46010	0.37090	0.30470	0.03500	0.16350	0.22420
Macro-algae	$r(i,j)$	0.02846	-0.00670	-0.01640	0.02778	-0.02691	-0.03416	0.03206
	Prob	0.14150	0.41450	0.27390	0.12980	0.01520	0.07760	0.11300
Reefscape B								
Massive non- <i>Acropora</i>	$r(i,j)$	-0.02224	0.00061	-0.06712	-0.05934	-0.00740	0.08073	0.06410
	Prob	0.22720	0.48900	0.11100	0.45900	0.38930	0.02640	0.04120
Branching <i>Acropora</i>	$r(i,j)$	-0.03157	0.01807	-0.05006	-0.08160	-0.00728	0.10701	0.00501
	Prob	0.14310	0.24510	0.45900	0.02040	0.36950	0.00700	0.39770
Sponges	$r(i,j)$	-0.05390	-0.04492	0.04363	0.14567	-0.03567	-0.05253	-0.05701
	Prob	0.45900	0.45900	0.45900	0.02880	0.07150	0.45900	0.45900
Branching non- <i>Acropora</i>	$r(i,j)$	0.05849	0.05046	-0.03305	-0.07971	0.02061	0.04246	-0.03295
	Prob	0.08150	0.03210	0.08880	0.03410	0.21750	0.45900	0.10240
Soft corals	$r(i,j)$	0.02042	0.03395	0.01598	-0.09084	-0.00188	0.01490	0.02137
	Prob	0.32090	0.10430	0.26690	0.00360	0.47200	0.29130	0.23020
Reefscape C								
Massive non- <i>Acropora</i>	$r(i,j)$	0.04433	0.02729	0.05063	-0.08892	0.03452	-0.00267	-0.05851
	Prob	0.11660	0.22870	0.07820	0.02890	0.13620	0.48310	0.12460
Sponges	$r(i,j)$	0.04815	0.02810	0.05138	-0.08876	0.03438	-0.00690	-0.05822
	Prob	0.10290	0.22640	0.07400	0.02890	0.13520	0.43770	0.13330
Soft corals	$r(i,j)$	0.05983	-0.01067	0.00996	0.05122	0.01548	-0.10390	0.01193
	Prob	0.06140	0.39050	0.38660	0.06130	0.35830	0.02890	0.40510
Foliose non- <i>Acropora</i>	$r(i,j)$	-0.01235	0.00480	0.00541	-0.07438	0.01283	-0.00172	0.12745
	Prob	0.35390	0.43180	0.43350	0.09300	0.41820	0.48860	0.03630
<i>Millepora</i>	$r(i,j)$	0.04870	0.02793	0.05119	-0.08836	0.03426	-0.00722	-0.05822
	Prob	0.09620	0.22650	0.07630	0.02890	0.13650	0.43190	0.13520
Digitate <i>Acropora</i>	$r(i,j)$	0.01341	-0.05033	-0.06975	0.10505	-0.03221	0.02305	0.00223
	Prob	0.34510	0.07700	0.11100	0.02700	0.12380	0.28500	0.48670
Capitate soft corals	$r(i,j)$	0.05983	-0.01067	0.00996	0.05122	0.01548	-0.10390	0.01193
	Prob	0.06310	0.39040	0.39010	0.06170	0.36250	0.02890	0.40310
Encrusting soft corals	$r(i,j)$	0.04870	0.02793	0.05119	-0.08836	0.03426	-0.00722	-0.05822
	Prob	0.09630	0.22790	0.07710	0.02890	0.13970	0.43400	0.13870

DISCUSSION

Different fish taxa or trophic groups having different ecological preferences in terms of food and shelter, and habitat partitioning among fish assemblages within a reef is common (Ohmans et al. 1997). However, at the scale of our individual sites at Davies Reef (50 m transects), the coupling between fish composition and benthic attributes is not tight (Figs. 6 & 7). The relationships between fish species richness, biomass and trophic structure were a little clearer. The encrusting non-*Acropora* reefscape (A), which had the largest proportion of massive non-*Acropora* corals, had the highest richness in species, highest total biomass and highest biomass of zooplankton feeders. The *Acropora* reefscape (B), with the highest *Acropora* cover, lowest non-*Acropora* and the highest cover of turf algae, had the highest biomass of herbivorous fishes. The ‘low coral’ reefscape (C) had a more even distribution of trophic classes and the lowest species richness. There is no obvious explanation for the even trophic class distribution within Reefscape C, but there could be a

cause and effect relationship between low coral cover and low fish species richness.

Geomorphology, depth and coral architecture also presumably act in concert to strongly partition fish assemblages. We found that mean fish species richness and biomass were higher on substrates dominated by hard corals providing vertical relief. This is not surprising given the 3D habitat structure and favourable habitats provided by high coral cover, and by branching structures in particular, for a number of demersal fish species (e.g. Bergman et al. 2000). As an example, Caribbean hard-bottom sites with a greater relative amount of 3D structure support over twice the mean species richness and diversity for fish as sand and sea-grass sites, and several times greater mean fish density (Kendall et al. 2004).

The relationship between coral reef fish abundance and richness and the cover of particular corals is very complex. Other studies have found contrasting relationships between fish abundance and richness and coral cover: a strong relationship (e.g. Bell & Galzin 1984, Bell et al. 1985, Findley & Findley 1985, Bou-

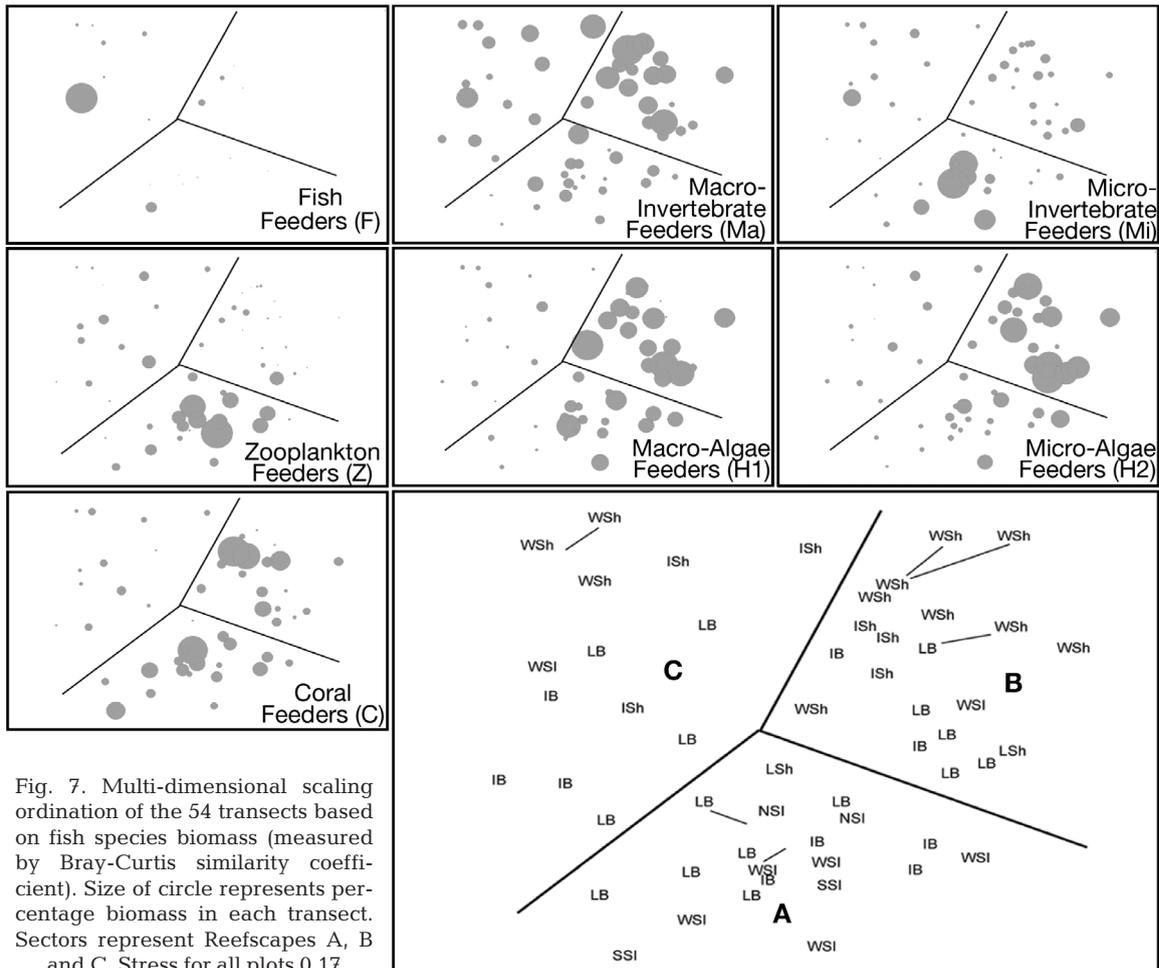


Fig. 7. Multi-dimensional scaling ordination of the 54 transects based on fish species biomass (measured by Bray-Curtis similarity coefficient). Size of circle represents percentage biomass in each transect. Sectors represent Reefscape A, B and C. Stress for all plots 0.17

chon-Navarro & Bouchon 1989, Nuñez-Lara & Arias-González 1998) or no relationship (e.g. Wellington 1992, Sale et al. 1994, Green 1996, Ohman & Rajasuriya 1998, Gust 2002, Lecchini et al. 2003). Lecchini et al. (2003) found that physical variables, including water depth, distance from shore and reef zone, all accounted for significant variation in the proportion of the structure of coral reef fish assemblages. This parallels the relationship that we found between fishes and reef zones, depth and aspect (Figs. 2 & 3).

While we found significant relationships between fish assemblages and benthic habitat, we found no simple strong relationship between fish assemblage composition and our measured benthic attributes of habitats. In a general sense, multiple cues appear to be driving the distribution of fish species and trophic groups. We could discern relationships between trophic groups and reefscales defined by grouped benthic attributes rather than a simple and strong relationship between fish assemblage composition and benthic attributes of habitats. For example, zooplankton feeders had a pronounced dominance in medium and deep reefscales (Reefscales A and C), while herbivores were dominant in shallow reefscales with low cover of algae, *Acropora* and sand (Reefscape B). The abundance of feeders on zooplankton, plant and coral were all correlated with benthic morpho-functional groups, but the abundance of fish feeders and invertebrate feeders was not. Legendre et al. (1997) described a globally significant relationship between reef bottom materials and feeding habits. In their study, herbivorous fish were over-represented in habitats with high live corals and calcareous algae; likewise, grazers and carnivores were over-represented in habitats high in coral debris, turf and dead coral, live coral, calcareous algae and other substrates. Copepod eaters were over-represented in habitats high in live corals and calcareous algae, whereas omnivores and piscivores did not exhibit any significant association with the substratum (Legendre et al. 1997).

Paradoxically, in our study, macro-algal feeders were under-represented in habitats that were high in 'algae, other', macro-algae and zoanthids. They were over-represented in sites high in encrusting *Acropora*. This finding suggests that macro-algal feeders keep algal biomass low in their preferred, encrusting *Acropora* habitat. A second group, micro-algal feeders, were over-represented in sites high in massive corals, encrusting corals, and branching *Acropora* with abundant algal turfs. Zooplankton feeders were under-represented in areas with high branching corals (both *Acropora* and non-*Acropora*), soft corals, encrusting soft corals, massive corals and *Millepora*, but over-represented in areas high in digitate *Acropora*. The latter are common in windward shallow habitats

exposed to currents or waves and where zooplankton washes onto the reef. Puzzlingly, coral feeders were over-represented amongst massive and foliose corals. Our study thus suggests a similar range of intuitive and non-intuitive relationships between fish assemblages and associated benthic communities as were found by Legendre et al. (1997).

Perhaps the most interesting result of this study is the capacity to extract spatial patterns of benthic life forms and depth from the fish assemblage ordinations and different analyses. Distribution patterns of fish assemblages closely followed patterns and gradients in depth, reef zone and benthic attributes. This relationship can be useful in 2 ways. First, the fish assemblage may be a useful indicator of benthic state, as well as of biotic and physical environmental gradients. Second, attributes of the benthic substratum that can rapidly be assessed may be useful proxies for predicting the type of fish community and its present state.

The multiple analysis approach used in this work was useful to extract distribution patterns of both fish and benthos. Coral reefs are extremely complex systems, and it is not an easy task to distinguish patterns and processes within them. Splitting the complex information of the system into different reefscales and making individual analyses in each reefscape has helped to define relationships between fish and benthic assemblages. This differential analysis allows structural and functional patterns to be explored as well.

Davies Reef is a very complex system with strong, diverse and spatially structured vertical relief, geomorphology, benthos and fishes. Despite such extreme complexity, it only required 2 response variables to explain most of the variation between fish assemblages: massive encrusting corals and branching *Acropora* corals. These same coral categories vary systematically with changes in wave energy across reefs (Done 1982), which is, in turn, related to depth and position on the reef.

The present study stresses the importance of habitat complexity as a requirement for rich and abundant fish assemblages. It is intuitive that loss of habitat structure and complexity due to human or natural impacts could reduce reef fish richness, in species and in biomass. We found that habitat characteristics affected the evenness and richness components of diversity differently: whereas, the *Acropora* reefscape was associated with high fish species evenness, massive encrusting corals were associated with high fish species richness and high biomass. However, its species diversity H' was low due to low evenness brought about by substantial over-representation of zooplankton feeders, mainly Pomacentridae.

In summary, we found that reef fishes at Davies Reef associate with each other in 3 recognisable, if overlapping, clusters. The clusters were most associated with the apparently different regimes of wave energy and turbulence characteristic of different reef zones and depths. There were some indications of fish relationships to the benthic composition and architectural complexity of the substratum. However, the latter attribute is relatively volatile, under the influences of disturbances such as the crown-of-thorns starfish, coral bleaching and storm damage. The fishes may thus cue more to the more perennial geomorphologic features such as spurs, grooves and ancient coral heads, than the more ephemeral, faster-growing elements that come and go over periods of months, years and decades.

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